The importance of species traits in biodiversity-ecosystem functioning research

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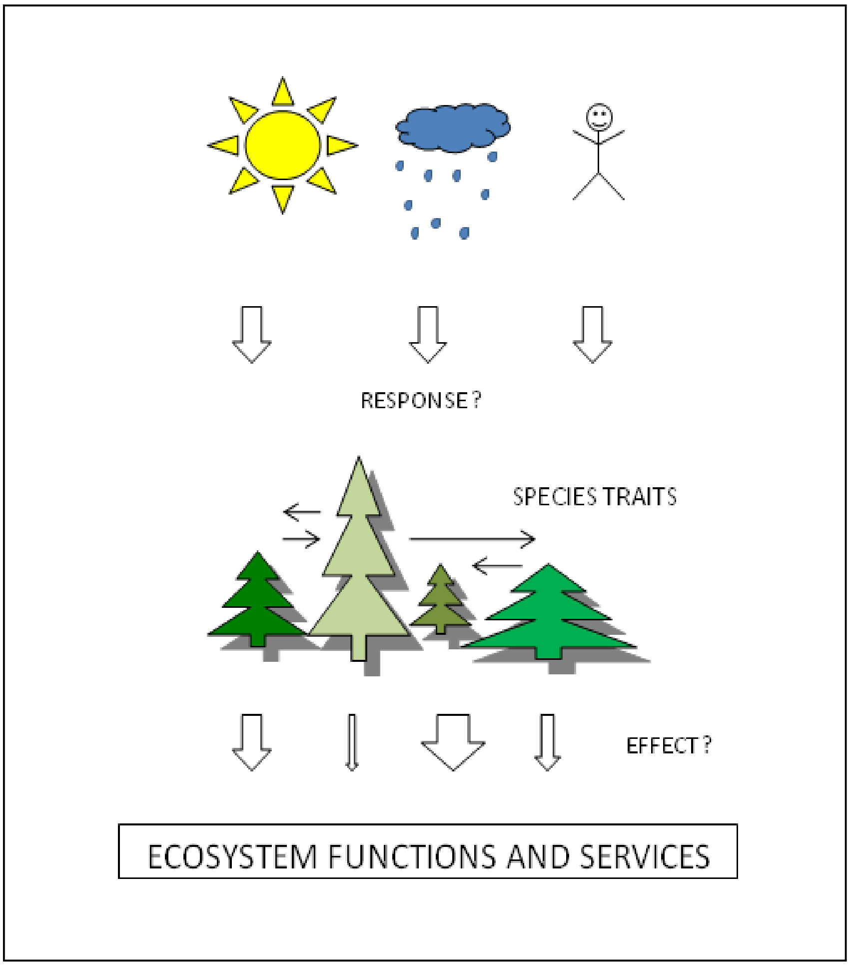

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Abstract

Biodiversity-ecosystem functioning research is a major field in ecology. Currently research on biodiversity and ecosystem functioning is shifting from focusing on species diversity to focus on functional diversity. From this point of views species traits play a central role, because it is the traits that determine how a species reacts to environmental change, and how this reaction influences ecosystem functions. In this essay, I present an overview over the nature and measurement of traits, and highlight examples of trait based approaches from different ecosystems. Despite that there is an increasing numbers of studies dealing with this topic, there is still confusion about the terminology of traits and functional groups. A new concept, dividing species traits into response- and effect traits seems to be a promising step forward. So far, focus has been placed on plants, because these are the most studied organisms in this field. Some key plant traits, such as leaf dry matter content (LDMC) and specific leaf area (SLA), are identified to be important factors determining species responses to environmental change, and seem to affect ecosystem functioning. Although decomposition is an ecosystem function of fundamental importance, the knowledge about soil communities is still limited. Despite that they are known to have considerable effects on decomposition rates, soil animal traits are rarely considered in decomposition studies. A change may, however be on its way, as the interest of the role of soil animal traits recently seem to be increasing.

1 Introduction

In the face of current environmental change and high rates of species extinctions, there is a growing concern about how to maintain ecosystem functions and services (Chapin *et al.* 2000). Although there are accumulating evidences that biodiversity govern ecosystem function and stability (Loreau *et al.* 2001; Hooper *et al.* 2005), the underlying mechanisms are still poorly understood. Questions on how much biodiversity is necessary to maintain ecosystems and how biodiversity is linked to ecosystem processes are of major priority for future well-being.

There is probably no single mechanism that could fully explain the observed relationship between biodiversity and ecosystem functioning. Several hypotheses about the shape of the relationship – from linear to idiosyncratic - have emerged during the last decades (fig.1)

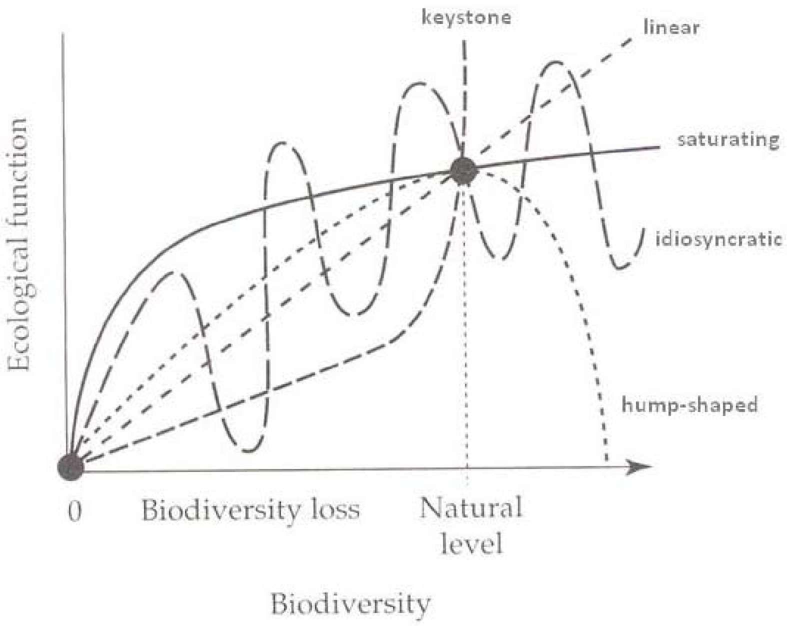

Figure 1 Some hypothetical trajectories of ecosystem function in relation to changes in biodiversity (re-drawn from (Naeem *et al.* 2009))

One sub-discipline within Biodiversity and Ecosystem Functioning (BDEF) research deals with the stability of ecosystem functioning and incorporates a temporal aspect. MacArthur (1955) developed a mathematical model from which a linear relationship between diversity and stability of energy flow is derived (MacArthur 1955). He found that more diverse communities in terms of trophic interactions have a greater ability to maintain species abundances due to the use of alternative energy paths. There is an enormous amount of literature dealing with the relationship between biodiversity and temporal stability of certain ecosystem functions. Within plant communities, evidence is accumulating for a positive relationship between species diversity and temporal stability of biomass production (Tilman & Downing 1994).

The second sub-discipline has a more spatial point of view, and is related to the idea of the niche concept. According to the “rivet hypothesis”, all species in a community are of equal importance. A loss of few species causes minor changes, but if a certain threshold is exceeded the ecosystem is collapsing (Ehrlich & Ehrlich 1981). Another possible explanation for the relationship between biodiversity and ecosystem functioning is the concept of redundancy. It assumes that there are species that are able to take over the function of lost species which leads to compensation. Thus, a minimum of diversity is needed to maintain function, while all other species are redundant. In addition, the insurance hypothesis states that the more different species are in their traits the less species are needed to ensure function of the ecosystems (Yachi & Loreau 1999). Dramatic decline in ecosystem function may occur also after small losses of biodiversity if key species are lost.

In contrast to the above mentioned hypotheses, Lawton & Brown (1993) postulated that losses of biodiversity may have unpredictable (idiosyncratic) consequences to ecosystem functioning due to lost interactions among species(Lawton & Brown 1993). Within experiments a decline in function following losses of biodiversity may also occur due to purely statistical reasons. With high species diversity, there is a higher probability that the randomly assembled community contains species important for a function. This type of effects are referred to as “sampling effects” (Huston 1997).

A resource based explanation for a positive biodiversity-ecosystem functioning relationship is represented by the complementarity effect (Loreau 1998). Resource partitioning and mutual species interactions cause a more effective total resource use.

A recent conceptual innovation is termed multifunctionality. It was proposed independently in two studies (Hector & Bagchi 2007; Gamfeldt *et al.* 2008). They state that the functional role of biodiversity might have been underestimated because the importance of ecosystem functions is usually considered one at the time. When more ecosystem processes were considered simultaneously, they observed that higher species diversity was needed to maintain a minimum rate of every process. Additionally, more species are needed if there is a lack of functional overlap among species (Hector & Bagchi 2007; Gamfeldt *et al.* 2008).

Plants are the most intensively studied organisms in this research field so far. Most support for a positive relationship between biodiversity and ecosystem functioning comes from studies of grassland ecosystems and the function of biomass production/productivity (Tilman & Downing 1994; Hector *et al.* 1999). But the positive biodiversity-ecosystem functioning relationship does by far not hold in every situation (Cardinale *et al.* 2000). Additionally, much less is known about the relationship in other important ecosystems.

In soil ecosystems, evidence is lacking for a positive role of species diversity on ecosystem functioning (Cragg & Bardgett 2001; Filser 2002). Despite the high biodiversity in soils, many species appears to be functionally redundant, as the biodiversity-functioning curves saturates already at relatively low diversity levels (Bardgett 2002). Hence, functional diversity and key stone species seem to play more important roles for ecosystem functioning (Mikola & Setala 1998; Setala 2002). This suggests that BEF research in soil communities need to focus more on diversity of functional traits than on species diversity. Currently, there is a general shift within the scientific community towards such trait-based approaches. Species performance within communities, and in relation to the environment, ultimately depends on the trait distribution and abundance of individual species (Naeem & Wright 2003). Dividing species into functional groups and comparing the performance of these groups with respect to a certain ecosystem function is a widely applied approach.

Functional groups appear to be useful tools to understand general mechanisms of complex systems, but difficulties to define and quantify these groups remains unsolved (Hooper *et al.* 2005). Moreover, multitrophic interactions, intraspecific variation (Reiss *et al.* 2009), and feedbacks between below and aboveground communities (Bardgett 2002) are increasingly considered to be important for ecosystem functioning.

In the following sections I intend to clarify the terms of functional diversity and traits, and shed light on the difficulties of defining functional groups and measuring traits. Furthermore I will give a general overview over trait-based concepts and approaches, which mainly stems from plant studies. Finally I will specifically review the importance of traits in soil ecosystem research, with emphasis on decomposition and soil animals.

2 Definitions

In general, a trait can be defined as surrogate of organismal performance, consisting of morphological, physiological, and phenological characteristics of an organism (Violle *et al.* 2007). Because species-environment interactions are of major interest, knowledge about the functional role of species and their interactions is required. In this respect functional traits can be defined as those phenotypical components of an organism that influence ecosystem properties or biogeochemical processes, and those that determine the response of an organism to environmental conditions (Lavorel & Garnier 2002; Hooper *et al.* 2005). These two types of functional traits are also referred to as effect- and response traits. There are different kinds of response traits. They can be related to resource acquisition, tolerance to abiotic environmental factors, or they can be linked to a species response to disturbance or to interactions with other organisms. Reproduction rate of an animal for example varies with varying environmental conditions such as temperature or moisture. Therefore it qualifies as response trait. A typical effect trait could be the mouth part morphology of a soil animal because it determines the comminution of plant litter and therefore influences decomposition.

It is also possible that a trait is both a response and effect trait. Feeding rate of a soil animal for example is influenced by climatic factors (increases with increasing temperature) and influences in turn the decomposition rate. Feeding rate is an example of both a response and effect trait.

It is also common to divide functional traits into hard and soft traits (Hodgson *et al.* 1999; Weiher *et al.* 1999). Hard traits capture the actual function, whereas soft traits are surrogates of the functions of interest that are easier to measure than the hard traits themselves. Dispersal distance is an example for a hard trait. In case of plants, a corresponding soft trait for dispersal distance could be seed mass. In the case of soil animals it could be leg length or mobility. Species that possess a common set of functional traits can be clustered into functional groups or functional types (Naeem & Wright 2003). The term functional diversity is commonly referred to as “the value and range of those species and organismal traits that influence ecosystem functioning” (Tilman 2001).

3 Difficulties in terminology and measurement of traits

Although trait-approaches are frequently used in ecological research consistency in the use of terminology and the underlying concepts is currently lacking (Violle *et al.* 2007). In a literature review Naeem & Wright (2003), critically look at the use of functional diversity in experiments. They found that most studies used subjective schemes to, *a priori*, assign organisms to certain functional groups based on e.g. life form or trophic position (Naeem & Wright 2003). Such classifications usually do not consider if the selected groups are influencing ecosystem function. This is the case when e.g. plants are classified according to their morphology (e.g. trees, shrubs, herbs). A related problem lies in the nature of defining distinct functional groups. How much should two species differ before they are classified as belonging to two groups? Boundaries between groups are often set arbitrary. It is more likely that species are located along continuous trait gradients rather than forming distinct groups (Hooper *et al.* 2005) depending on biotic and abiotic factors. This implies that traits are context specific, which means that the contribution of traits to community performance is likely to vary with environmental conditions (Fox & Harpole 2008). Again the classification into functional types appears to be problematic.

The functional types recognized to be important for one ecosystem property may not have the same importance in other ecosystem properties (Hooper *et al.* 2005). Species traits can also differ between different life stages (Lavorel & Garnier 2002). A further complication is that diversity effects on functioning may depend on the temporal scale of the study (Hillebrand & Matthiessen 2009).

Petchey et al. (2010) mention six frequently used measures of functional diversity. The convex hull volume or CHV determines the volume that covers a set of points (species) in n-dimensional trait space (Cornwell *et al.* 2006). The FD_{var} is the variance of trait values measured by the sum of squared deviations from the weighted (by abundance) mean of the species (Mason *et al.* 2003). Another group of measures use distance as measure of functional diversity. Mean diversity (MD) (Heemsbergen *et al.* 2004) and functional attribute diversity (FAD) (Walker *et al.* 1999), use the mean distance between species in a multivariate space. Rao`s quadratic entropy (Q), uses pairs of species to calculate the sum of the product of their distance and abundance (Botta-Dukat 2005).

FD (Petchey & Gaston 2002) and Podani and Schmera`s modified FD termed FD_{LD} (Podani & Schmera 2006) are based on dendrograms where the functional diversity is measured as branch length. In their simulation model, Petchey et al. (2010) showed that the different approaches all resulted in similar estimates of functional diversity. Thus, they argue that for assessing the importance of diversity, it is more important to focus on how many traits are important for the particular function in question, than focusing on how to measure the diversity of traits. An important issue, however, is that the different measures allow for different relationships between species richness and functional diversity. This is caused by the different nature of the measures. For example, the value of FD, CHV and the FD_{LD} measures generally increase with species richness, while the diversity value of the MD, Q and FD_{var} measures can increase if a species richness is decreased.

Table 1 Different measures of functional diversity. Some measures allow for an increase in functional diversity not only when species diversity increases but also when species are lost. A “+” indicates that this is allowed and a “–“ indicates that it is not allowed for the specific measure.

measure based on		increase with species loss allowed
Volume in trait space		
	CHV	-
Variance		
	FD_{var}	+
Distance		
	MD	+
	FAD	+
	Q	+
Dendrogram		
	FD	-
	FD_{LD}	-

4 Plant trait approaches

4.1 The concept of response and effect traits

The concept of response- and effect traits (Lavorel & Garnier 2002) is currently receiving much attention. Although studies identifying either traits relevant to responses or relevant to effects are numerous, only a few studies have so far made the step to relate response and effect traits (Walker *et al.* 1999; Engelhardt 2006; Quetier *et al.* 2007). Hence identification of key traits that determine the response to environmental change, and their effects on different ecosystem function, remains a challenge. Traits, such as growth rate and tissue life-span, mineral nutrient concentration, defense against herbivores, and resistance to decomposition have been suggested as promising candidates that may play a key role in driving ecosystem processes (Diaz *et al.* 2004).

Community composition results from a hierarchical sorting process due to biotic and abiotic constraints for species/traits persistence. According to the biomass ratio hypothesis the relative importance of specific traits for ecosystem functioning is assumed to be proportional to the biomass that represents the trait in question (Grime 1998; Diaz & Cabido 2001). However, in many cases, a single trait, or a group of traits can be of disproportional large importance (Lyons *et al.* 2005). Suding (2008) presents three types of possible relations between response and effect. First, effect and response can correlate (or effect and response traits can be identical), resulting in either positive or negative correlation between response and effect traits. A negative correlation will occur if the traits that contribute most to the ecosystem function also are the most sensitive to the environmental change. A positive relationship occurs if the traits which are most sensitive to environmental change are less important for the ecosystem function. Second, an overlap in response and effect could occur. This occurs when all traits contribute equally to the ecosystem function, but differ in their reaction to environmental change. This will result in insurance against diversity losses due to functional redundancy (Lavorel & Garnier 2002). Third, there is the possibility of no correlation between response and effect. This may occur if traits that relate to regeneration (fecundity, dispersal), which are not considered important for ecosystem functioning, are the ones that respond most to the changed environment (Lavorel & Garnier 2002; Suding *et al.* 2008). In addition, to make matter even worse, interactions among species may result in large difference between the trait performance identified for single species and the trait performance of the whole community (Reiss *et al.* 2009).

Klumpp & Soussana (2009) performed a mathematical test of the framework developed by Suding et al. (2008), and were able to demonstrate that changes in disturbance (grazing intensity) caused changes in ecosystem function (aboveground productivity, C-flux), through changes in certain traits (Klumpp & Soussana 2009). Root traits such as specific length, tissue density, and diameter responded to change in disturbance, and had significant effects on C-fluxes.

Regarding leaf traits, the functional divergence (distribution) of traits like specific leaf area (SLA) and leaf dry matter content (LDMC), were affected by grazing, and predicted changes in aboveground productivity and C-fluxes. This study confirms that theoretical framework, such as the one presented by Suding et al. (2008), can be used for realistic scaling of effects from species to communities, and thereby predict effects at the ecosystems.

4.2 Within-and among –community trait variation

Combining functional diversity with community assembly theory and ecological strategies by dividing trait variation into within and among community components is another interesting direction (Ackerly & Cornwell 2007) . In their framework Ackerly & Cornwell (2007), divide plant trait diversity into an alpha- and a beta component, similar to Whittaker's alpha and beta diversity (Whittaker 1972). The beta determines a species' position along a gradient of community means of a trait. The alpha component is represented by the difference between a species' trait value and the beta value. The alpha value therefore measures how the traits of a species differ from co-occuring species in a particular community. An advantage of this method is that it can be applied even if no environmental data are available, because the ordination of communities and species is based on trait values. They also show that the relationship among traits can differ between different spatial scales. For example, a strong correlation can occur among communities caused by a response to the same abiotic gradient, but these traits could be uncorrelated at the "within-community level" where patterns are driven by co-occurance mechanisms. To predict future changes in ecosystem function, it is necessary to scale up from single species and individual ecosystems to the regional, landscape, and global scale.

5 Decomposition

Decomposition is fundamentally important for recycling of carbon and nutrients (Swift 1979) because organic bound nutrients are converted into a mineral form and returned into the soil.

Litter decomposition rate is controlled by multiple factors, including environmental conditions like temperature and precipitation (Trofymow *et al.* 2002), the chemical litter quality and the decomposer community present (Cornelissen 1996; Aerts 1997).

5.1 Leaf litter traits influence decomposition

Differences in decomposition rate are often reported to be related to leaf litter traits such as leaf toughness, C:N ratio C:lignin ratio, nitrogen, lignin, or polyphenol concentrations (Berg & Staaf 1980; Perez-Harguindeguy *et al.* 2000). More recent studies emphasize the importance of leaf mass per area (LMA), or leaf dry matter content (LDMC) (Kazakou *et al.* 2009). Although climate creates similar conditions for litter decomposition within biomes, variation in decomposition can be much larger within a climate region than between climate regions (Cornwell *et al.* 2008). In a world-wide meta-analysis, Cornwell et al. (2008) identified species specific traits as the predominant drivers of variation in decomposition rate.

Studies on the effect of different leaf litter mixtures on decomposition rate increased only recently (Moore & Fairweather 2006; Pérez Harguindeguy *et al.* 2008). As for single species the LDMC seems to play an important role in community assemblages, and turned out to be negatively correlated to decomposability (Quested *et al.* 2007; Fortunel *et al.* 2009). Other studies show that decomposition rates increases with increasing plant species diversity (Zimmer 2002), or increasing functional group diversity (Scherer-Lorenzen 2008), or increasing diversity of chemical compounds (Meier & Bowman 2008). The majority of studies, so far, indicate a non-additive effects of plant litter diversity on leaf litter decomposition (Gartner & Cardon 2004). The most likely mechanism for such non-additive patterns involves a nutrient transfer from high - to low quality leaves, which leads to an increased decomposability of the more recalcitrant litter, either by leaching (Briones & Ineson 1996) or by fungal hyphae (Tiunov 2009).

Studies in compliance with the response and effect trait concept are still rare within the litter decomposition literature. However, Fortunel et al. (2009), identified that certain leaf traits (LDMC and leaf nitrogen content) captures the effect of land use change and climate, as well as the effect on litter decomposability.

5.2 The role of soil fauna in decomposition processes

Causes for the tremendous biodiversity in soil ecosystems are still poorly known. A possible explanation is that competition is reduced through multi-dimensional niche partitioning (soil heterogeneity, species differences in response to abiotic factors, starvation in unfavorable conditions) (Bardgett 2002). In a global decomposition experiment, Wall et al. (2008) showed that in addition to climate, soil animals play a fundamental role in regulating decomposition rate. Soil animals mostly contribute to decomposition through litter fragmentation which influences the microbial community. Although it is known that soil invertebrates have a large impact on soil functioning (Lavelle *et al.* 2006) there are no consistent pattern concerning the relationship between soil animal diversity and belowground process rates. It has been shown that species diversity *per se* does not enhance below ground processes (Griffiths *et al.* 2000). Such processes are rather assumed to be driven by functional group diversity, species identity (Huhta *et al.* 1998) or functional dissimilarity among species (Heemsbergen *et al.* 2004). Currently, there is a growing number of studies dealing with these questions. For example, Hedde et al. (2007) identified functional groups of macro-arthropodes according to traits based on their effect on beech leaf degradation. In a follow-up study Hedde et al. (2010) combined morphological traits (body length, weight, comminution apparatus) and effect traits (defaecation rate, C content, C:N ratio of faeces) to investigate the relationship between trait dissimilarity and leaf degradation. In that study they found a positive relationship between minimum trait dissimilarity and leaf mass loss. In a study examining the combined effect of litter quality, elevated CO_2 and elevated temperature on feeding by the millipede *Glomeris marginata,* Rouifed et al. (2010) demonstrated that the identity of litter species and feeding of *Glomeris marginata* played a major role for litter mass loss (Rouifed *et al.* 2010). Another study demonstrated that leaf litter mass loss and soil respiration is positively correlated with a high functional dissimilarity of the macrofauna (Heemsbergen *et al.* 2004).

6 Conclusions and Perspectives

Species traits are shown to play a key role for ecosystem functioning. They determine species` reaction to a changing environment, which can lead to an altered community composition. Such changes can potentially influence key ecosystem functions. This means that species traits are the link between the response of species to the environment and their effect on ecosystem functioning. Facing current environmental change many ecosystem functions and services are seriously threatened. Trait based approaches dealing with biodiversity-ecosystem functioning relationships have therefore become a major subject in modern ecology research. A future task will be to get a more mechanistic insight into the role of traits. A useful contribution is to determine key traits and establish trait databases for different organism groups. Although a growing body of research is focusing on trait-based questions results are still biased towards plants in terrestrial ecosystems in contrast to other organisms and ecosystems. Concerning the lack of consistent terminology major improvements can be seen in the recent development.

As decomposition is of crucial importance for nutrient cycling and an important part in the C-cycle more emphasis should be placed on factors influencing decomposition rates. As for other ecosystem functions the decomposition research with respect to traits is still biased to studies on leaf litter traits combined with climatic parameters. Soil animals are often ignored although they can have profound direct- and indirect effects on decomposition. Hence, I argue that they should be included in future decomposition models and experiments.

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